THE STRUCTURE AND SIGNIFICANCE OF VESTIGIAL WINGS AMONG INSECTS.

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Although considerable attention has been paid by entomologists to the structure and development of the wings of insects, but few observers have ever given any careful descriptions of insect wings which are in a vestigial condition. The well-marked constancy of the wing structure and its use as an aid to classification has long been recognized, so that one can not fail to suspect *a priori* that there should be a considerable range of variation in the structure of vestigial[1] wings. That the wings are exceedingly important organs has never been questioned, indeed, it is a generally accepted view that they are one of the most important factors in making the Insecta such a dominant group, and the causes which induce their atrophy must undoubtedly be deep-seated. Moreover, from the extent of degeneration it should be possible to obtain some knowledge as to the length of time during which such causes may have been acting. How far such a method may be relied upon, it is my present desire to show.

In a recent paper upon the reduction of wings among the Diptera Bezzi ('00) has shown that there are two categories into which we may divide such Diptera accordingly to the apparent cause of the wingless condition, viz.: First, cases brought about by external parasitism. Second, those induced by a secluded environment. It is possible to include almost all the general types of wingless insects under these two heads, except in a few cases where other influences seem to be at work.

The examination of a number of myrmecophilous Hymenoptera and Diptera has called my attention to the fact that several rather clearly defined types of vestigial wing structure may be

[1] The term vestigial is here used instead of rudimentary. The latter word has often been employed in this connection by entomologists, but with evident impropriety, as it should apply in its strict sense only to organs still in process of ontogenetic development.

recognized. Extending these observations to include other insects also, it seems possible to distribute all these cases into three categories as follows:

1. Wings having essentially a pupal character, *i. e.*, developing as normal wings up to the pupal stage but failing to expand.

2. Wings essentially normal, except for their smaller size and less complex venation; sometimes even developing a color pattern, or possessing unique and quite distinctive characters.

3. Wings consisting of little more than a hollow bag and giving no clue from their appearance as to the probable wing structure of their ancestors. (Comparable in a way to the halteres of the Diptera.)

Of these three groups, the first would seem to indicate the most recently acquired brachypterous condition, and the third apparently the one just preceding the totally apterous state. The latter should therefore be phylogenetically the oldest.

The Trend of Phylogenetic Development in Subapterous Forms.

In flying insects where the wings are of supreme importance their structure is very constant for each form; but as soon as they become vestigial to such an extent that they are no longer available for their only function, that of flight, they are a useless burden, so that once this stage has been reached natural selection should rapidly remove them entirely. This is no doubt the case, for insects with wings just too short for use in flight are very rarely met with. Of these exceptions two groups can be defined:

1. Forms where the wings have suddenly developed characters which make them of use in some other direction.[1]

2. In groups which seem to be undergoing rapid and remarkable phylogenetic changes, *e. g.*, the Phoridæ among the Diptera.

The great preponderance of the forms which have wings of the third type (vide *supra*) shows that there is a rather sharply defined point where they become so vestigial that they are no

[1] Examples of this can be seen in widely separated groups. A notable case is that of a chalcid fly, *Eupelmus rhizophelus*, considered in the sequel.

longer acted upon by natural selection. This also is seen in widely separated groups, *e. g.*, Coleoptera (*Zopherus*) and Diptera (*Ecitomyia*), where the wing is simply a slender, hollow bag of very simple structure.

The fact that in this extremely reduced state they resemble the halteres of Diptera is interesting as affording evidence from another source that the halteres are the vestiges of the second pair of wings which have acquired the new function of equilibration in the Diptera.

The Causes Inducing the Atrophy of the Wings.

Recently Dewitz ('02) has published the results of some experiments upon certain wasps (*Polistes*), where he succeeded in obtaining artificially, specimens of the *Polistes* with abortive wings. These were obtained by subjecting the young larvæ to a low temperature for a considerable period, by laying the nest upon a cake of ice. After undergoing this treatment while still young the insects developed only the stumps of wings on attaining the adult state. Whether the low temperature in this case acts in a way especially to retard the development of the wings other than by causing a general weakness of the body seems to me very doubtful. The anlagen of the wings are present in the pupa and the last and supreme act of an insect on casting off its pupal skin is properly to expand its wings. If its store of energy has been depleted by untoward conditions during its larval life they are the parts which become abnormal. Thus expansion may take place only imperfectly or not at all if the organism has not vigor enough to expand them. I have known artificial conditions of various sorts such as extreme dryness and hot, damp air in closed jars to cause specimens with deformed wings. Under natural conditions such freaks also occur, although much more rarely. During the past summer I have collected a specimen of *Ammophila urnaria* and also one of *Sphex pennsylvanica*, in which the wings were very small and much deformed. Such abnormalities are, however, fundamentally different from normally reduced wings and their structure is not constant. Moreover, such sudden variations without corresponding changes in habits can never be preserved by natural selection.

Dewitz[1] associates a diminution of the oxidation processes in the body with the wingless condition, which is borne out by the comparative anatomy of the tracheal system, but as to which is cause and which effect it is not so easy to decide. As actively flying insects require more air to aërate their blood, they naturally have more extensive tracheæ and respiratory sacs to supply it, so that it seems only proper to consider that in isolated genera or species among a winged group of insects it is the wings and not the tracheæ hidden inside the body which have first been influenced by external conditions and caused to change their form.

In the case of males of certain species which are winged while the females are wingless the short life of the male and the necessity of his seeking the female are sufficient to account for the female being the sex to lose the wings first in becoming adapted to the environment.[2]

It has long been recognized that insects inhabiting certain regions are more apt to be wingless or subapterous than their relatives living under other surroundings; notably the forms inhabiting oceanic islands, mountain tops and of deserts or arid regions tend to have the wings short or wanting. These seem to be the only anomalous cases, for all others can be traced to parasitism or secluded environment. The well-known explanation of Wallace that the great numbers of insects blown out to sea and thus destroyed has caused forms that do not fly or are wingless to be saved at the expense of the more active forms, is regarded by Dewitz ('02) as having little weight. It is true that actual observations upon this point are not numerous, but the immense numbers of dead insects that are often cast up on beaches after a severe storm show that this must be a very important factor. Needham ('00) has given interesting data upon this subject in a recent paper on the insect drift of Lake Michigan in which he describes the enormous numbers of insects cast up on certain portions of the beach of Lake Michigan.[3]

Isolated mountain peaks present similar conditions, although here the mortality can not be so great. A windstorm in such

[1] *Loc. cit.*

[2] See also note under *Dicælus*, page 187.

[3] Leconte has described similar phenomena on Lake Superior beaches.

a locality would more readily remove them from their proper environment than in the lowlands, and consequently from conditions favorable for the growth of their offspring. This would favor wingless forms.

As wingless insects are rarer in cold than in warm regions, the cold does not seem to be a possible factor.

The wingless condition of desert forms has never, I think, been satisfactorily explained, although it is the expression of a well-marked tendency.[1]

A secluded environment very often induces the atrophy of wings. This is seen most strikingly among myrmecophilous and cave insects. There can be but little doubt that in such cases wings are nearly always an inconvenience or even danger. Thus we find that all blind insects are also wingless, wings being evidently detrimental to safety when unguided by vision.

The influence of external parasitism apon the wings is so well recognized that it need only be recalled in the present connection.

From the fact previously alluded to, that the loss of wings is at first very rapid and then suddenly becomes extremely slow when they have reached a very vestigial condition, it can be readily seen that attempts to ascertain the phylogenetic age of a certain wingless type must be very difficult except in a very few cases. Added to this the great differences in plasticity among the widely separated groups with which we have to deal add further difficulties. Nevertheless, by comparing the various cases considered in the second portion of this paper, it is readily seen that the loss of wings must be very readily brought about, for nearly every apterous or subapterous form has a closely related form living under apparently nearly the same conditions, which is winged. Moreover, the loss of wings is usually accompanied by only slight changes in the external morphology of the insect.[2]

[1] In this connection it may be mentioned not as a full explanation, but as a fact which may bear upon this question; that in wingless coleoptera such as *Eleodes* and allied forms the tight-fitting and immovable elytra must prevent to a great extent the evaporation of water from the body and thus enable them better to withstand long and severe droughts. The fact that *Eleodes* also occurs in certain moist regions can be understood when we remember that arid regions seem to be the centers of distribution for such forms.

[2] In many apterous coleoptera a correlated change is the shortening of the metathoracic or wing-bearing segment.

Thus the causes must be such as affect the wings alone. It seems therefore that we may be justified in saying that it is the result of certain mechanical influences of the environment affecting the wings alone, which causes their loss. This may be accomplished either by hindering the organism in its movements [1] or by laying it open to removal from its proper environment.[2]

First Category, "Pupal" Wings.

Where the development of the wings proceeds normally up to the formation of the pupa and is then suddenly arrested, the adult wings resemble those of the pupa in general detail and form except that they are more heavily chitinized. They occur in certain flies belonging to the family Phoridæ [3] and indicate the first step toward their total atrophy. The species with this form of wings resemble more closely in other morphological details fully winged forms than do their relatives whose wings fall into the second and third categories.

The cases of wingless grasshoppers afford beautiful examples of this persistence of the wing character of the previous instar. In these Orthoptera the wings of subapterous species cannot be distinguished from those of the earlier instars of fully winged species by structure alone. Were it not for the fact that there is a reversion of the relative positions of the two pairs of wings [4] at the last ecdysis one could not decide from a mere examination of the wings whether a certain form is larval or adult.

Empyris subapterus M. et B. MSS., ♀ (Proctotrupidæ) (Fig. 2).

The wings of this species, like those of many other Proctotrupidæ, are very short, but still retain a nearly normal system of neuration. The wing membrane has been lost, while the venation remains undisturbed. This gives the wings a distinctly pupal character.

[1] That the wings are an inconvenience to life under certain conditions is evinced by the well-known fact that the fertile queens of ants actually tear off the wings on beginning their underground life.

[2] In the cases of insects inhabiting small oceanic islands, mountain tops and deserts, the possible habitat for a species is usually very limited.

[3] Notably the genera *Psyllomyia* Lw. and *Commoptera* Brues.

[4] In all instars except the last, the posterior wings lie above the anterior ones, which position is reversed in the adult.

Megaspilus sp. indescr. (Proctotrupidæ) (Fig. 3).

In a small subapterous species of *Megaspilus* is seen the very common phenomenon of a micropterous species closely resembling other fully winged forms. Many other cases of this could be cited among this group of Hymenoptera.

Apteropompilus (?) sp. indescr. (Fig. 4).

In a most remarkable nearly wingless species of Pompilidæ which occurs in Texas, the venation is more complex than that of *Empyris*, but much simpler than in other genera of Pompilidæ. In this case the wings are very small, being scarcely visible without a strong lens and the thorax is narrower than usual, due doubtless to the slight devolopment of the wing muscles. In this family no intermediate forms are known between this and the fully winged species, all of which fly with great activity. Running has taken the place of flight, a tendency which is seen in many of these sand-wasps which are fully winged.

Second Category.

The following examples have been chosen to illustrate the condition of wings which are much reduced in size, but still retain very well-defined and distinctive characters.

1. *Mutilla grandiceps* Blake, ♂ (Fig. 1).

This species of *Mutilla* is a rare exception among the males of this genus of velvet ants, for like the females of all species, it is incapable of flight. Among all the three or four hundred species of this cosmopolitan group, the rule of wingless females and perfectly winged males holds with only two or three exceptions. From the figure it can be seen that the wings are well proportioned and still retain the hooks upon the anterior margin of the hind pair. The venation is much confused and not plainly defined. The wings while very small in comparison to the size of the insects (reaching scarcely to the tip of the thorax) recall very strongly the normal wings of certain Proctotrupidæ and Chalcididæ where the venation is often completely lost.

2. *Henicopygus subapterus* Ashm. (Chalcididæ) (Fig. 6).

The wings of this insect are very small and evidently useless for flight, but nevertheless have a very distinct venation properly pro-

portioned to their size and exhibit a sharply defined color pattern of hyaline and fuscous patches. They are normal wings in miniature.

3. *Eupelmus rhizophelus* Ashm. (Chalcididæ) (Fig. 7).

One of the most remarkable modifications which I have observed occurs in this insect. The wings which are much reduced in size are suddenly bent upwards at a right angle near the middle and project like two great spines at the apex of the metathorax. The basal half is testaceous in color and flat, while the raised extremities are black and somewhat curled with acute tips. What their function may be I will not venture to suggest, but their extraordinary form leaves little doubt that they are adapted to some special use.

4. Numerous Diptera, *e. g.* Phoridæ (see Brues, '02) and the genus *Termitoxenia*, Wasmann (Fig. 10) show remarkable modifications of the wings which evidently fulfill secondary functions in these insects.

Third Category.

Although all wings falling into this group are necessarily without salient characters, they show a considerable range of variation, which is not apparently correlated, however, with their systematic relationships.

1. *Pasimachus punctulatus* Hald. (Coleoptera) (Figs. 12, 13, 14).

In this carabid beetle the wings are larger than in *Dicælus* (see below) and their larger size is accompanied by a more elaborate form and much greater range of variation, as can be seen from the accompanying figures. They have apparently not yet reached the final minimum size and simple shape. By mounting the wings of specimens which have been preserved in formalin, in glycerine jelly, the tracheation of the wing can be readily made out. A drawing made from such a preparation is shown in Fig. 14. The form of the single trachea was found to be almost identical in several wings; it is a simple tube and not dendriform except for a few slender branches at the tip and at irregular intervals near the middle of the wing where the diameter of the trachea is greatest. The tænidia are very distinct and the tube is considerably coiled upon itself, being somewhat longer than the wing. The development of the wing nervures has evidently

been stopped soon after the trachea began to push out into the wing, and the subsequent changes in the trachea not taking place, it has retained its primitive structure. The persistence of a trachea in this manner with its tænidium in an adult insect wing does not seem to have been previously recorded and is especially interesting in this case as it shows the retention of a distinctly pupal character in the imaginal instar; *i. e.*, of arrested development in the wing and not of perfect development on a smaller scale.

2. *Dicælus splendidus* (Coleoptera, Carabidæ) (Fig. 16).

In this form the wings are similar in the two sexes. They are short, slightly over two millimeters in length or one-sixth the body length, and broadly attached to the integument of the metathorax at their bases. The basal articulation is broad and not at all flexible, and as the wings themselves are very strongly chitinized, they remain immovably fixed and cover the postero-lateral angles of the metathorax. The membrane forming the dorsal wall of the first abdominal segment is pushed inward to give space for the wing, which is quite thick.

Since the other species of this genus, which are winged, make but little use of their wings, it is natural to expect that here both sexes would have the wings reduced to an equal degree, for we are not dealing with a male which flies in search of the female. This points to the idea that it is the difference in the necessary activities of the two sexes that usually causes the male to retain the power of flight longer than the female, and not an inherent morphological or physiological tendency as has been suggested.

3. *Eleodes* sp. (?) (Coleoptera) (Fig. 17).

One of the common Texan species of this large Tenebrionid genus which was examined has extremely short, often bilobed wings which appear simply as slightly projecting protuberances of the metathoracic wall. *Eleodes tricostata* Say and other species have very similar wings.

4. *Zopherus* sp. (?) (Fig. 11).

In this strange Tenebrionid we do not find, as might be expected from the complete coalescence of the elytra, a complete absence of wings. There are structures several millimeters in length, forming thin and delicate flattened sacs which usually

show two sharp transverse creases, and very different from the stumps of thick chitin seen in *Eleodes.*

4. *Ecitomyia Wheeleri* Brues (Fig. 9).

The simple type of a hollow bag is seen here in its plainest form, the wing is slightly curled so as to be convex dorsally and concave below, while the upper side is covered with scattered bristles. Otherwise it is structureless. Another Dipteron, *Eretmoptera* recently described by Kellogg has small wings very similar to those of *Ecitomyia.*

Explanation of Plate.

FIG. 1. Wing of *Mutilla grandiceps* Bl. ♂.

FIG. 2. Wing of *Empyris subapterus* (M. et B. MSS.), ♀.

FIG. 3. Wing of *Megaspilus* sp. indescr.

FIG. 4. Wing of *Apteropompilus* (?) sp. indescr.

FIG. 5. Wing of a subapterous Braconid. (Chelonus.)

FIG. 6. Wing of *Henicopygus subapterus,* ♀, Ashm.

FIG. 7. Wing of *Eupelmus rhizophelus,* ♀, Ashm.

FIG. 8. Wing of a micropterous ♂ of *Isogenus nubecula.* (After Sharp.)

FIG. 9. Wing of *Ecitomyia Wheeleri* Brues, ♀.

FIG. 10. Wing of *Termitoxenia Heimi* Wasm. (♀ ?). (After Wasmann.)

FIG. 11. Wing of *Zopherus* sp.?

FIG. 12. Wing of *Pasimachus punctulatus.*

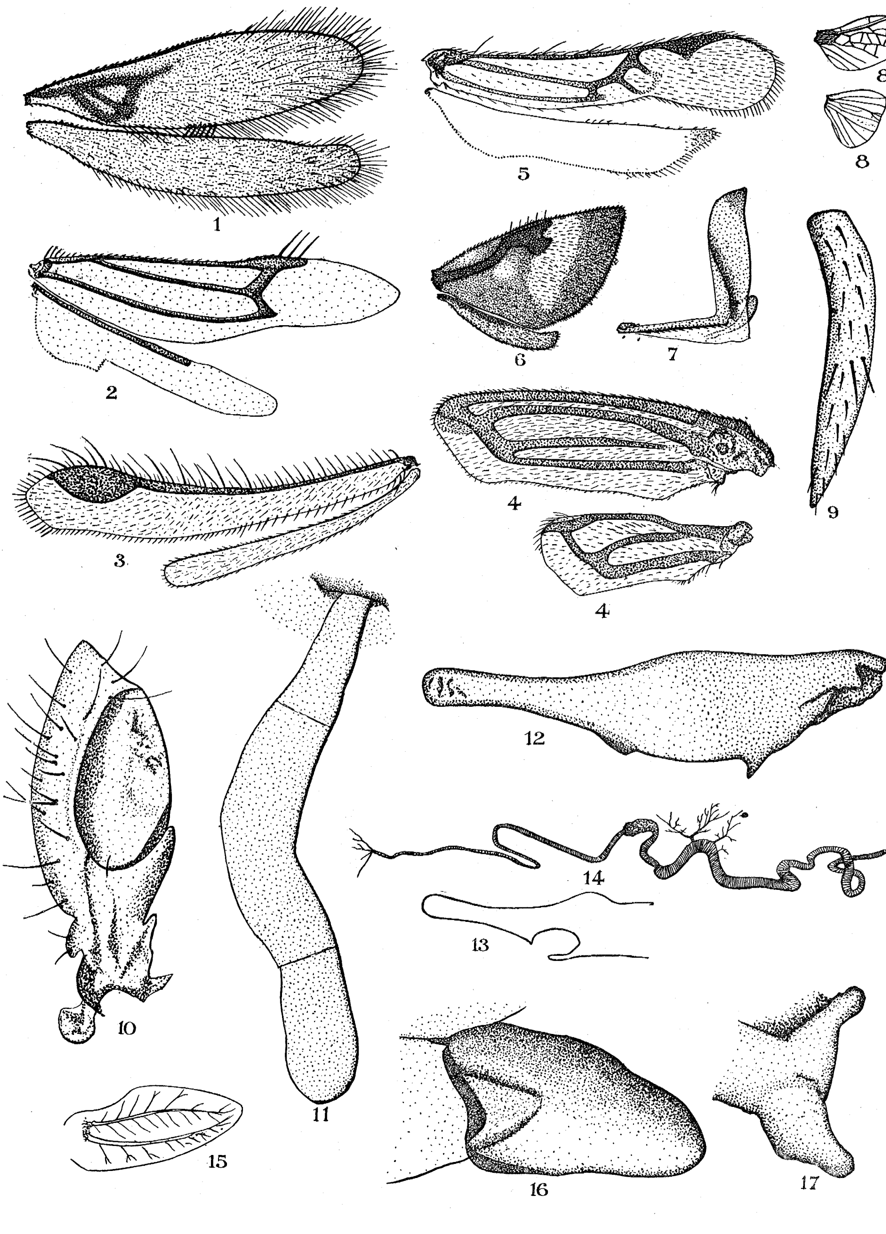
FIG. 13. Wing of *Pasimachus punctulatus,* less enlarged.

FIG. 14. Tracheation of apical part of wing shown in Fig. 12.

FIG. 15. Wing of *Pœcilium affinis,* ♂. (After Sharp.)

FIG. 16. Wing of *Dicælus splendidus.*

FIG. 17. Wing of *Eleodes* sp. (?).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